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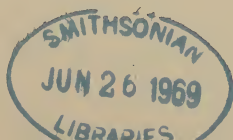
PROCEEDINGS
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TWO ADDITIONAL SUBSPECIES OF NORTH
AMERICAN CROTALID SNAKES,
GENUS *AGKISTRODON*

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Investigations leading toward a monographic review of the genus *Agkistrodon* Beauvois, 1799, have indicated that the recognition of some additional subspecies will tend to make the pattern of geographic dispersal and probable evolutionary history of the group more easily interpreted. In this paper a fifth subspecies of the copperhead, *A. contortrix* (Linnaeus), and a third subspecies of the cottonmouth, *A. piscivorus* (Lacépède), are described. In outlining these subspecies, a large number of specimens has been examined in each case, but since it is not feasible to deal here with the entire hypothesis, diagnoses and definitions are based on a small series selected from the central portion of the geographic range of each.

It has been pointed out (Gloyd and Conant, 1943, p. 147) that both the copperhead and the cottonmouth, as species, are exceedingly homogeneous in structural characters but that geographic races are recognizable on the basis of differences in color and pattern. Such differences, however, are often supported by average (mean) differences in at least some morphological attributes. The several subspecies now recognized are easily distinguished from each other throughout most of their respective ranges, but there are many areas in which individuals are obviously intermediate; intergradation appears to occur wherever any two adjacent subspecies are in contact. The keys to the subspecies included here are based upon all



data presently available to the writer and, along with consideration of the geographic ranges given, should identify individuals other than those definitely intermediate; i. e., at least 75 percent in each of the respective populations. Discussion of geographic and evolutionary relationships is reserved for a detailed treatment of the genus. Names of museums abbreviated in the text are listed on page 231.

***Agkistrodon contortrix phaeogaster* new subspecies**

OSAGE COPPERHEAD

Figure 1

Agkistrodon mokeson mokeson, Gloyd and Conant, 1943, Chicago Acad. Sci. Bull., vol. 7, no. 2, p. 150 (part).

Agkistrodon contortrix mokeson, Klauber, 1948, Copeia, no. 1, p. 8 (part).

Holotype: United States National Museum no. 165955, adult male, received from Dr. Henry S. Fitch, July, 1960; locality 10 miles south of McLouth, Jefferson County, Kansas; collector not stated.

Paratypes: The following, all from east-central Kansas: Douglas County, USNM 165958-9, 7 mi. SE of Lawrence; AMNH 102614-5, FMNH 178997-8, UMMZ 128842, 3 mi. NW of Lawrence, UCM 36348, 7 mi. SW of Clinton. Franklin County, USNM 165956-7, Gould's Ford, Middle Creek, 3 mi. S and 3 mi. E of Ottawa. Jefferson County, KU 120336-7, 12 mi. N of Lawrence. Johnson County, AMNH 102616, UMMZ 128843, 2 mi. S of Stanley. Miami County, USNM 165960-1, Miami County State Lake. All specimens here mentioned were collected by Dr. Henry S. Fitch and his associates at the University of Kansas, particularly Robert Fleet, Richard Hayworth, William Kerfoot, Roy and Dennis O'Connor, and Eric Schulenberger, 1960-63.

Diagnosis: A population of copperheads in which the crossbands of the body are (1) generally in sharp contrast with the ground color; (2) have dark edges narrowly bordered with white, extending down the sides to, or almost to, the ventrals; and (3) are 3 to 5 scales wide at the midline and 6 to 11 scales wide where they are in contact, or nearly so, with the ventrals (Fig. 1). There are usually no small dark spots or blotches in the ground color between the crossbands. The ventral markings are irregular gray to black blotches, mostly in contact, extending across the belly and producing a dusky, marbled or clouded pattern, sometimes quite dark. The yellow tip of the tail of juveniles is replaced by yellowish green and this color is retained by most adults.

Description of Holotype: Top of head with nine symmetrical scutes characteristic of the genus, with the frontal aberrant: a longitudinal suture divides it, separating on the right side a narrow extra scale about one-fourth the total width of the frontal; also a transverse suture separates a minute scale at the posterior midpoint of the frontal. Each parietal has a dark spot of pigment near its mesial border and back of each of these a

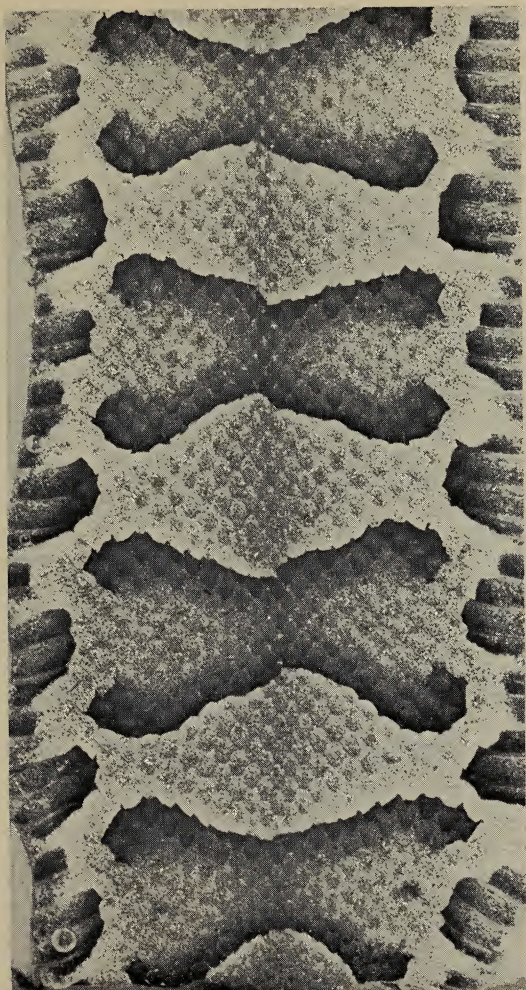


FIG. 1. *Agkistrodon contortrix phaeogaster* new subspecies. A paratype, USNM 165957, Gould's Ford, Franklin County, Kansas.

short groove extends anterolaterally for about one-third the width of the scute. Nasals two, the anterior one larger. Loreals one on each side, large, higher than wide. Preoculars two, the lower one forming the upper posterior border of the pit. Postoculars (including suboculars) 5 on the left side, 4 on the right. A small postfoveal between lower preoculars and anteriormost postoculars, making a total of 9 scales in the orbit on the left side and 8 on the right. Supralabials 8-7, the second forming the anterior border of the pit, the fourth largest and separated from the orbit by the two anteriormost post(sub-)oculars. An anterior postfoveal forms the lower posterior border of the pit. Infralabials 10 on the left side, 9 on the right. Temporals in 6 or 7 irregular rows; the large scales of the lowest row, 4 on the left and 3 on the right, conspicuously larger than all the others and without keels. The first pair of infralabials in broad contact behind the mental. One pair of enlarged chin shields. Median gulars in 3 irregular pairs; lateral gulars in 5 to 6 oblique rows.

Dorsal scales all strongly carinate on body and tail, and each with two apical pits. Scale rows 27-25-23-21, the order of decrease (Dowling recount system, 1951) as follows:

$$\begin{array}{ccccccc}
 & -7(15) & & -5(22) & & -5(123) & \\
 27 & \text{---} & 25 & \text{---} & 23 & \text{---} & 21 \quad (148) \\
 & -7(16) & & -5(22) & & -4(103) &
 \end{array}$$

Ventrals 148; anal plate not divided. Both hemipenes everted. Subcaudals 46, the proximal one and the distal 16 divided. There is a vertical scar from a healed wound on the right side of the body on scale rows 4 to 8 opposite ventral 87, and an indication of a slight injury on the top of the snout at the meeting point of the internasals and prefrontals.

Total length 990 mm; tail length 125 mm; tail/total length ratio .126.

General coloration in life rich tones of brown: reddish brown on top of the head and in the crossbands of the body, with the ground color a lighter tone of brown; after preservation faded to corresponding tones of darker and lighter grayish brown. Muzzle and top of head uniform, with no trace of pattern; a darker tone of brown extending down over the temporals forms an indistinct cheek stripe which is outlined below by a narrow dark brown line edged with cream color; this extends obliquely backward from the orbit across the lowest row of temporals and downward across the last supralabial to the commissure. At the sides of the muzzle above the nares a narrow dark line on the edges of the internasals and nasals. Supralabials, lower portions of first row of temporals, and upper halves of infralabials cream color, densely stippled with brown. A sharp narrow line of dark brown extends backward from the second infralabial across the middle of the infralabials to a point just below the angle of the mouth; here it curves downward and outlines the pale tan pattern of the lower jaw and throat; this area is slightly darker than the ventral ground color and is densely stippled with fine dots of brown and gray.

Dorsal ground color grayish brown, with much fine stippling of

brown and gray. A pattern of dark brown crossbands, all extending down the sides and making contact with the ventral scutes. There is a half-band on the left side between the first and second crossbands, the next nine crossbands are complete, then follow two half-bands on the left and one on the right, then two irregular complete bands, a half-band on the right, and a final band complete but irregular. Thus a count of half-bands on the sides gives 16 on the left and 15 on the right. The crossbands vary from 5 to 8 scales wide at the base and 3 to 5 scales wide at the midline; they are darker at the borders and narrowly edged with light cream (or white). There are no dark spots or blotches in the ground color between the crossbands. The tail has one complete band proximally, then an irregular zig-zag pattern followed by a dark terminal spine.

Ventral ground color cream to pale tan with fine dark stippling throughout the length of the body. A ventral pattern of broad dark brown blotches, confluent mesially and extending irregularly toward the sides where the outer portions are darker, the whole giving a dusky, marbled effect, darker anteriorly and becoming progressively lighter toward the tail. Under surface of the tail with dense dark stippling, distally becoming almost black.

Notes on Paratypes: Minor variations from the usual scutellation of the head include irregular sutures in the parietals extending laterally from the mesial plane part way across the scutes. The parietals are usually truncate posteriorly. The frontal often with small scales separated off the anterior and/or posterior midpoints, or off the anterolateral angles (corners). Supralabials usually 8, occasionally 7; infralabials 9 or 10, occasionally 11. Preoculars 2, a small postfoveal usually entering the orbit below them. Postoculars (including suboculars) 4 or 5. Ventrals 143-149 (146) in 7 males, 143-150 (146) in 9 females. Subcaudals 45-47 (45.7) in males, 39-46 (43.1) in females. Divided subcaudals 11-22 (males), 10-28 (females). Tail/total length ratio .137-.155 (.146) in males, .129-.147 (.139) in females.

In the 16 specimens of the paratype series the crossbands of the body range from 12 to 14; in two the 14 crossbands are complete and symmetrically continuous across the body; in the others there are irregularities of incomplete bands in which from one to several half-bands alternate or make only partial contact at the middorsal line. On the tail are 1 to 4 proximal crossbands similar to those on the body, followed by a dark zig-zag pattern or by a series of 8 or 9 crossbands decreasing in size and distance apart distally; terminal spine with 1 or 2 transverse black bands.

In ten of these specimens, medium-sized adults, a lyre-shaped pattern on the top of the head and the sides of the neck is more or less clear. This is a forward continuation of each of the lateral points of the first crossband (on the neck) to become confluent with the dark cheek stripe extending forward to the orbit, and expanding mesially into rounded extensions two to four scale-widths back of the parietals. Such a pattern

is not evident in large adults in which the entire top of the head, including the postparietal region, is uniform copper-brown.

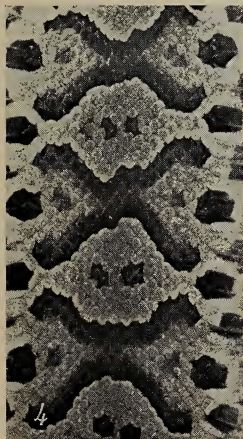
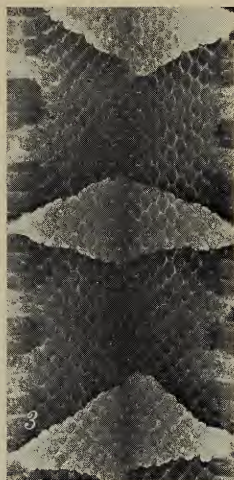
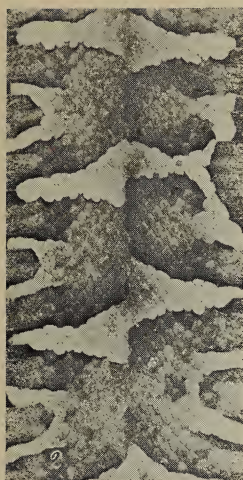
The ventral coloration is similar to that described for the holotype except for variation in intensity of pigmentation; the belly pattern of USNM 165957 (Fig. 1) and USNM 165961 is considerably darker, appearing brownish black anteriorly.

The name *phaeogaster* alludes to the dusky, dark gray to black, mottling of the belly.

Geographical distribution: *A. c. phaeogaster* occupies the major portion of the Marais des Cygnes-Osage River drainage system in eastern Kansas and central Missouri. It intergrades with *A. c. laticinctus* in southern Kansas and northern Oklahoma, and with *A. c. contortrix* from southern Missouri northward along the Mississippi River to southeastern Iowa.

KEY TO THE SUBSPECIES OF THE COPPERHEAD

1. Dorsal pattern of the body consisting of broad dark crossbands, not much narrower middorsally than on the sides (more than half as wide at the midline as on the lowest lateral scale rows), extending across the lateral ends of the ventral scutes and more or less continuous with the dark markings of the belly 2
- Dorsal pattern of the body consisting of dark crossbands (or alternating half-bands) considerably narrower middorsally than on the sides (usually less than half as wide at the midline as on the lower lateral scale rows), and not continuous with the dark markings of the belly 3
2. Belly very dark, heavily mottled, sometimes almost uniform black; crossbands with three dark ventrolateral areas each continuous with the dark color of the belly (Fig. 2); tail relatively long, about 17 percent of total length in males, 14 percent in females; subcaudals 48-62 (54) in males, 42-57 (49) in females
pictigaster Gloyd and Conant, 1943.
 Trans-Pecos Texas (Jeff Davis, Presidio, Brewster, and Terrell counties) and adjacent areas to the east (Crockett and Val Verde counties).
 Belly not conspicuously dark; crossbands with three dark ventrolateral blotches extending onto the ventral scutes but tending to become weak toward the middle of the belly (Fig. 3); tail about 14 percent of total length in males, 13 percent in females; subcaudals 42-54 (47) in males, 40-51 (45) in females
laticinctus Gloyd and Conant, 1934.
 South-central Texas (Frio and Calhoun counties) northward through central Oklahoma to southern Kansas (Cowley County).
3. Crossbands extending down the sides to the ventral scutes or to the lowermost row of dorsal scales, but not continuous with the dark irregular blotches of the belly, and without three ventrolateral blotches or spots within or immediately adjacent to them (Fig. 1); belly pattern irregularly mottled or marbled, more dusky ante-



FIGS. 2-5. 2, *A. c. pictigaster*, a paratype, CA 7807, Oak Spring, Chisos Mountains, Brewster County, Texas. 3, *A. c. laticinctus*, holotype, UMMZ 75599, 26 mi. NW of San Antonio, Bexar County, Texas. 4, *A. c. mokasen*, USNM 166134, Scioto County, Ohio. 5, *A. c. contortrix*, CA 5089, Gentilly, Orleans Parish, Louisiana.

riorly; no small dark spots in dorsal ground color between crossbands *phaeogaster*, new subspecies.

See *Geographic distribution* above.

Crossbands not extending down the sides to the ventral scutes, but fading out or rounding off on scale row two or above 4

4. Crossbands somewhat "dumbbell-shaped," moderately restricted at the middorsal line (here usually 3 to 5 scale-lengths in width); a series of dark ventrolateral spots on the lowermost dorsal scale rows and the edges of the ventral scutes, one opposite the middle of each crossband and the adjacent ones between the crossbands, and all of about equal intensity; usually a secondary pattern of small to medium-sized dark spots dorsally between the crossbands, sometimes singly, often in pairs (Fig. 4) ... *mokasen** Beauvois, 1799. Southern Illinois and northeastern Mississippi northeastward to Massachusetts; throughout the Appalachian mountain region, and intergrading with *contortrix* across a broad area of the piedmont and Atlantic Coastal Plain. An upland form.

Crossbands somewhat "hourglass-shaped"; greatly restricted at the middorsal line (here 2 or 3 scale-lengths in width), often irregularly divided, the half-bands not meeting middorsally but alternating on opposite sides of the body; a series of ventrolateral spots not of equal intensity, those opposite the middles of the crossbands pale and diffuse, those alternating between the crossbands dark and well-defined; no secondary pattern of small dark spots dorsally between the crossbands (Fig. 5); both ground color and pattern generally pale *contortrix* Linnaeus, 1766. Mississippi Valley, Gulf and Atlantic Coastal Plains, from southeastern Texas north to east-central Missouri and western Illinois, and to southern Maryland in the east, exclusive of peninsular Florida. A lowland form.

***Agkistrodon piscivorus conanti* new subspecies**

FLORIDA COTTONMOUTH

Figure 6

Agkistrodon piscivorus piscivorus, Gloyd and Conant, 1943, Chicago Acad. Sci. Bull., vol. 7, no. 2, p. 166 (part), fig. 6, 14, and 16.

Holotype: United States National Museum no. 165962, a young adult male, collected 16 July 1966, "at edge of Rochelle-Cross Creek Road, about 7 miles southeast" of Gainesville, Alachua County, Florida, by R. P. Elliott, J. Wariner, and P. Pinnel.

Paratypes: USNM 165963, AMNH 102618, Paynes Prairie, about 5.5 mi. S of Gainesville, Alachua County; USNM 165964, Hampton, Bradford County; FMNH 178999, 5 mi. E of Andalusia, Flagler County; AMNH 102617, UCM 36350, Waccasassa River, 0.5 mi. S of State Road 24, Levy County; and FMNH 179000, 5 mi. NE of Palatka, Putnam

* For explanation of return to this spelling, see Smith and Gloyd, 1964.

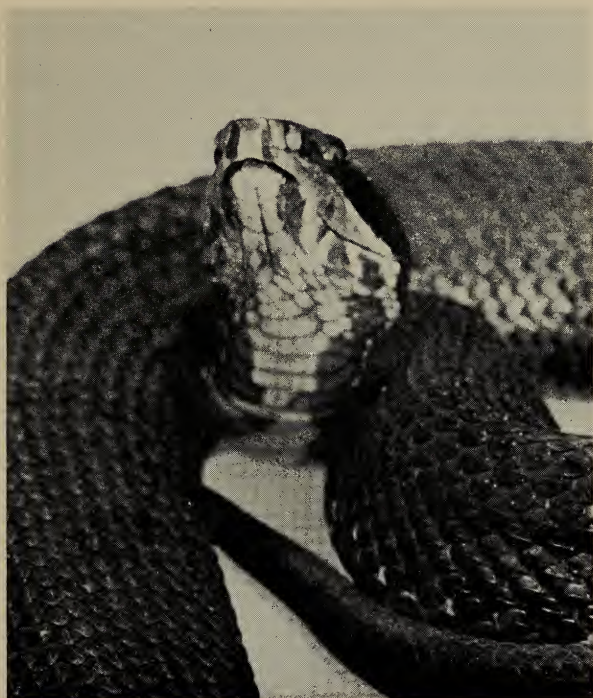


FIG. 6. *Agkistrodon piscivorus conanti* new subspecies. CA 11346, Florida, exact locality unknown.

County, Florida. The specimens in this series were collected by Dr. W. J. Riemer, J. A. Holman, Norm Tessman, and W. G. Weaver, Jr. of the University of Florida.

Diagnosis: The distinguishing characters of this subspecies most readily utilizable are the strong, sharply defined markings of the snout and head, even in most relatively large (old) individuals: a dark brown cheek stripe outlined above and below by a distinct light line (white or cream); a conspicuous vertical dark stripe on the sides of the rostral and the adjacent prenasals and supralabials (Fig. 6); dark markings on labials above and below the commissure, more numerous below; and a pair of longitudinal dark stripes on the lower jaw, on the first two or three infralabials and the edges of the chin shields.

Differences in proportions as expressed in number of ventrals and sub-

caudals and relative length of tail here support the differences shown in the coloration (e. g., males of this population have tails considerably longer than those of the other two subspecies), and these data will be presented later in a detailed consideration of variation within the species.

Description of Holotype: Top of head with the nine symmetrically arranged scutes characteristic of the genus but with modifications as follows: a small triangular scute at each anterolateral point of the frontal; a narrow elliptical scale between the frontal, left supraocular, and left parietal; a single triangular scale occupying the notch between each parietal and its corresponding supraocular. Each parietal truncated by a transverse suture separating the posterior third. Two nasals, the posterior extending forward into the nostril. No loreals. Two preoculars, the lower one smaller, forming the upper posterior border of the pit, and having a suture-like groove across the posterior tip near the orbit. A very small postfoveal entering the orbit on each side. Two postoculars, the upper one small, the lower crescent-shaped and forming the lower posterior border of the orbit. Supralabials 8, the second extending upward to form the anterior border of the pit, the third largest and extending upward to form the lower anterior border of the orbit. A small postfoveal forms the lower posterior border of the pit. Infralabials 10 on the left side, 11 on the right. Temporals in five longitudinal rows at a point opposite the posterior ends of the parietals; the scales of the lowest row larger, and the anterior two of these without keels. The posterior tips of the first infralabials extend backward between the chin shields of which there is one pair. Four rows of median gulars, the two inner ones less than half the width of the outer ones; five or six irregular rows of lateral gulars.

Dorsal scales each with two conspicuous apical pits, and all strongly keeled on body and tail. Scale rows 27-25-23-21, the order of decrease (Dowling recount system, 1951) as follows:

27	—	7(12)	25	—	6(107)	23	—	6(129)	21	(141½)
	—	7(12)		—	6(107)		—	5(130)		

Ventrals 141, plus a half one on the right side. Anal plate not divided. Both hemipenes everted. Subcaudals 50, the proximal 34 and the 37th single (undivided), the 35th, 36th, and the distal 13 in pairs (divided). There is a scar from a wound in the skin on the right side opposite ventrals 41-45. Total length 795 mm; tail length 142 mm; tail/total length ratio .178.

Top of head dark brown in frontal and parietal region, pale brown on outer margins of internasals, prefrontals, and supraoculars. Muzzle generally light. Sides of head, lower jaws, and throat cream to white and conspicuously marked with dark brown as follows: sharply defined vertical bars on the sides of the rostral and the adjacent edges of the prenasals and first supralabials; a short dark stripe from the posterior edge of the postnasal obliquely downward across the preoculars and postfoveal

to the orbit; a broad dark cheek stripe, sharply defined above and below with white, extending obliquely backward from the orbit and beyond and beneath the angle of the jaw, covering the upper edges of the supralabials, the lowest row of temporals, and the lower halves of the temporals of the second row; a triangular spot at the sutures between the 1st and 2nd, 3rd and 4th, and 4th and 5th supralabials; a dark stripe from the mental obliquely backward across infralabials 1 to 5 and the outer edges of the chin shields; and dark spots at the sutures of infralabials 5 and 6, 6 and 7, and 8 and 9.

Dorsal coloration of body pale brown with 12 dark brown crossbands, the ground color becoming darker posteriorly and dark brown to black on the tail. The crossbands are 8 to 11 scales wide on the sides (on scale rows 4 or 5) and 6 to 8 scales wide middorsally; they are dark brown at the margins, pale brown in the central portions, which here are only slightly darker than the ground color, and contain one or more irregular dark blotches on the sides. The margins of the crossbands extend onto the ventrals as dark areas to correspond with a separate series of small blotches and thus form an irregular row of dark ventrolateral spots on each side.

The tail is generally dark brown to black above and below, except the distal half which is cream to white below; it is crossed by approximately 10 indistinct dark bands. The belly is cream-colored anteriorly, but this becomes obscured by dark pigmentation toward the tail.

Notes on Paratypes: The seven paratypes range in size from a subadult male (total length 396 mm) to a moderately large adult female (1055 mm). All show the sharply defined diagnostic pattern of the head. In structural characters there is only slight variation: supralabials 8-8 in all; infralabials 10 or 11; preoculars 2-2 with a small postfoveal entering the orbit; postoculars 2-2 or 3-3, in one instance 3-4. Ventrals, two males, 136, 141; five females, 132-138 (136); subcaudals, males, 47, 50; females, 42-46 (44); divided subcaudals, males, 13, 16; females, 12-24 (18). Tail/total length ratio, males, .169, .183; females, .158-.178 (.161).

A body pattern of broad crossbands is distinct in all, but in the largest of the series it becomes obscured posteriorly by darker pigmentation which also involves the ground color. Crossbands 13 in males, 11 to 13 in females, 4 to 8 scales wide at the midline, 7 to 11 scales wide on the sides; darker at the edges, with central areas little different in tone from the ground color and usually with dark blotches of varying size and intensity. Occasionally irregular half-bands alternate instead of meeting evenly at the midline. Both ground color and crossbands become progressively darker posteriorly. In all except the subadults the crossband pattern of the tail is obliterated, and with increasing size (age) the tail becomes black above and below. When the pattern of the tail can be seen, there are 8 or 9 irregular crossbands and the tip is light, sometimes with a trace of yellow. The ventral ground color is white, cream, or pale tan, darker in younger individuals. The ventral markings are

blotches or spots of reddish brown, brownish black, or black, stronger toward the sides, more distinct in younger individuals, and usually flowing together posteriorly into a nearly continuous black area in older ones.

This subspecies is named in honor of a friend and colleague, Roger Conant, Director of the Philadelphia Zoological Garden, whose professional achievements and dynamic promotion of the study of herpetology for amateurs merit highest commendation.

Geographic distribution: The range of *A. p. conanti* includes all of Florida and its off-shore islands and the southern part of Georgia. Intergradation with *A. p. leucostoma* occurs in southwestern Alabama, and with *A. p. piscivorus* in southeastern Alabama and southern and southeastern Georgia.

KEY TO THE SUBSPECIES OF THE COTTONMOUTH

1. Tip of the snout conspicuously marked by a pair of dark vertical lines at the edges of the rostral and the adjacent prenasals and first supralabials (Fig. 6); markings of the head usually sharply defined, except in some large (old) individuals; tail relatively long, averaging 18 percent of the total length in males, 16 percent in females; subcaudals 45-54 (50) in males, 41-49 (45) in females
..... *conanti*, new subspecies.

See *Geographic distribution*, above.

- Tip of the snout without dark vertical lines at the edges of the rostral, adjacent prenasals and first supralabials; markings of the head usually not sharply defined except in juveniles; relative length of the tail averaging 16 percent in males, 15 percent in females 2
2. Top and sides of the snout dark brown or black with no visible pattern; general coloration relatively dark, even in juveniles; subcaudals 38-49 (44) in males, 36-48 (42) in females
..... *leucostoma* (Troost), 1836.

The Mississippi Valley from southeastern Kansas, central Missouri, southern Illinois, western Kentucky, and western Tennessee south to the Gulf of Mexico; west to central Oklahoma, west central Texas, and along the Gulf Coast from the vicinity of Corpus Christi Bay east to southern Alabama.

Top and sides of the snout generally light brown, no pattern of lines or stripes; general coloration relatively light; crossbands of body usually in strong contrast with the ground color; subcaudals 39-51 (46) in males, 41-50 (44) in females
..... *piscivorus* (Lacépède), 1789.

Atlantic Coastal Plain from east-central Alabama and eastern Georgia to southeastern Virginia.

Acknowledgments: For assistance in obtaining living specimens from selected localities in Kansas and Florida I am indebted to Dr. Henry S. Fitch, Dr. William J. Riemer, Dr. Walter Auffenberg, and William G.

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Names of Museums Abbreviated in Text

- AMNH—American Museum of Natural History, New York
 CA—Chicago Academy of Sciences
 FMNH—Field Museum of Natural History, Chicago
 KU—University of Kansas, Museum of Natural History, Lawrence
 UCM—University of Colorado Museum, Boulder
 UMMZ—University of Michigan Museum of Zoology, Ann Arbor
 USNM—United States National Museum, Washington, D. C.

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